

If a few trials with large numbers of spikes are overlooked (as would happen if, for example, the assumed variance was smaller than the true variance), then the number of triplets predicted will be too low. The results are not as sensitive to changes in the PSTH. Low-pass filtering the PSTH does not affect the predicted triplet structure as long as frequencies below about 30 Hz are not attenuated. This corresponds to smoothing the PSTH with a Gaussian having a standard deviation of ~5 ms, which is equivalent to grouping spikes in 30 ms wide time bins.

DISCUSSION

A spike train has many degrees of freedom, and the idea that many of them might carry information is appealing. However, the results reviewed above show that accurately describing spike trains requires specifying only (a) the spike count distribution (which is approximately truncated Gaussian), (b) the PSTH (with a bandwidth of less than 30 Hz, the equivalent of measuring spike counts in 30 ms wide bins), and (c) the interval histogram. If they completely describe single neuronal responses, then these features contain all of the information that is available from those responses, no matter what representation is chosen. The accuracy of the spike count matched model shows that the fine temporal structure of responses (here triplets and quadruplets repeating within and across trials) depends stochastically only on these coarser measures. Thus, the fine temporal structures should be viewed as a transformed representation of the response.

Given these findings, one can wonder whether these precisely timed structures could be used to enhance information transmission. That possibility seems unlikely to us. The information carried by these patterns is already available from the spike count (and from the slowly varying temporal variation seen in the PSTH). Furthermore, the amount of information carried by the triplets is much less than that carried by the spike count, because per trial, the number of triplets is much more variable than the number of

spikes. There are large numbers of trials that have few or no repeating triplets and a few or a single trial with a large number of repeating triplets, sometimes hundreds. This variability is even greater for any particular triplet type. Such a large variance makes these triplet patterns a code that is less reliable than spike count. Thus, the triplets (and other precisely-timed patterns) are poor candidates for carrying critical information.

This work clearly demonstrates that the fine temporal structure of a spike train is sensitive to the distribution of spike counts (Fig 5C). Poisson distributions have often been assumed to be effective models of the response. If we consider sufficiently narrow time bins and assume that spikes appear in each independently of all the others, a Poisson process arises naturally. This appealing derivation and the mathematical tractability of the Poisson process have contributed to the widespread use of Poisson models of spike trains. These models predict a Poisson distribution of spike counts in sufficiently long time windows. Experimental data, however, including that presented here, have generally been inconsistent with the Poisson hypothesis (Baddeley et al., 1997; Berry, Meister, 1998; Bradley et al., 1987; Britten et al., 1993; Buracas et al., 1998; Gershon et al., 1998; Lee et al., 1998; Levine, Troy, 1986; Reich et al., 1997; Snowden et al., 1992; Tolhurst et al., 1989; Victor, Purpura, 1996; Vogels et al., 1989). A correlation between time bins, such as that observed in Heller et al (1993), shows that the Poisson assumption cannot be correct.

We conclude that the spike trains are consistent with a stochastic process generating all the spikes, and that serial correlation on a broad time scale (spike count distribution and PSTH) can give rise to the fine temporal structures seen in the data. In another context, Brindly (1998) has shown that slow correlations in spike counts between pairs of neurons can give rise to narrow cross-correlogram peaks (a type of precise correlation). Thus, the existence of structure at fine time scales does not imply control at fine time scales. Accounting for the influence of correlations over long periods on precisely timed patterns of any type found in spike trains is always